



RESEARCH ARTICLE

Saproxylic species are linked to the amount and isolation of dead wood across spatial scales in a beech forest

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Abstract

Context Dead wood is a key habitat for saproxylic species, which are often used as indicators of habitat quality in forests. Understanding how the amount and spatial distribution of dead wood in the landscape affects saproxylic communities is therefore important for maintaining high forest biodiversity.

Objectives We investigated effects of the amount and isolation of dead wood on the alpha and beta diversity of four saproxylic species groups, with a focus on how the spatial scale influences results.

Methods We inventoried saproxylic beetles, wood-

inhabiting fungi, and epixylic bryophytes and lichens on 62 plots in the Sihlwald forest reserve in Switzerland. We used GLMs to relate plot-level species richness to dead wood amount and isolation on spatial scales of 20–200 m radius. Further, we used GDMs to determine how dead wood amount and isolation affected beta diversity.

Results A larger amount of dead wood increased beetle richness on all spatial scales, while isolation had no effect. For fungi, bryophytes and lichens this was only true on small spatial scales. On larger scales of our study, dead wood amount had no effect, while greater isolation decreased species richness. Further, we found no strong consistent patterns explaining beta diversity.

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Conclusions Our multi-taxon study shows that habitat amount and isolation can strongly differ in the spatial scale on which they influence local species richness. To generally support the species richness of different saproxylic groups, dead wood must primarily be available in large amounts but should also be evenly distributed because negative effects of isolation already showed at scales under 100 m.

Keywords Biodiversity conservation · Connectivity · Forest management · Habitat amount hypothesis · Scale dependence

Introduction

Biodiversity is declining globally as a consequence of climate and land-use change (Sala et al. 2000; Rockström et al. 2009; Steffen et al. 2015; IPBES 2019). Forests cover about one-third of the global total landmass (FAO 2010; FOREST EUROPE 2015), and in temperate regions a high proportion of species depend on them, e.g. around 40% of the species in Switzerland (Imesch et al. 2015; Rigling and Schaffer 2015). Forest management therefore plays an essential role in the conservation of biodiversity (FAO 2010). While tropical forests are disappearing rapidly, European forests have been expanding since the 1990s but are often intensively managed (Bryant et al. 1997; FAO 2010). This leads to a severe underrepresentation of old successional stages in many regions (Vilén et al. 2012) and a decline of species that depend on old-growth forest characteristics such as large amounts of dead wood and old trees (Brunet et al. 2010; Paillet et al. 2010; Eckelt et al. 2018). In temperate and boreal regions, 20–25% of forest species depend on the availability of dead wood (= saproxylic species; Stokland et al. 2012), which makes it a key element for biodiversity conservation in forests (MCPFE 2003; Stokland et al. 2012). Preserving biodiversity consequently requires not only the presence of forested area, but also management that preserves such habitats within forests. For the development of appropriate management concepts, research on key elements supporting biodiversity is needed.

Conservation measures often aim to increase habitat availability for species, which can be reached through an increased habitat amount (Margules and

Pressey 2000). Complementing the amount, the spatial distribution of habitats is regarded as another key factor to preserve species (Tschardt et al. 2012). To improve conservation measures, it is therefore also necessary to understand how habitat configuration fosters biodiversity. MacArthur and Wilson (1967) developed the theory of island biogeography, stating that the species richness of an island depends on its size and isolation, which has implication in conservation when managing habitats. In particular, this concept has been adopted to manage patches of habitat in fragmented terrestrial ecosystems (Tschardt et al. 2012; Fahrig 2013; Watling et al. 2020). However, Fahrig (2013) questioned this application and proposed the ‘habitat amount hypothesis’, stating that in a ‘local landscape’ (of appropriate size) only the habitat amount affects species richness. According to this hypothesis, species richness is not influenced by the isolation and the size of the ‘local patch’ where species are sampled, but rather by the ‘sample area effect’ driving the two effects (for details see Fahrig 2013). While some studies testing the habitat amount hypothesis have found support for it (e.g. birds: De Camargo et al. 2018; small mammals: Melo et al. 2017; macro-moths: Merckx et al. 2019; saproxylic beetles: Seibold et al. 2017; multiple species: Watling et al. 2020), others have rejected it (e.g. plants: Evju and Sverdrup-Thygeson 2016; Lindgren and Cousins 2017; micro-arthropods: Haddad et al. 2016; birds: Kormann et al. 2018) or found different results for different taxonomic groups (frogs and reptiles: Pulsford et al. 2017). Studies testing the habitat amount hypothesis need to disentangle habitat amount and isolation, which is not always easy in natural ecosystems, as the two factors are often highly correlated (Fahrig 2017). Besides species richness, habitat amount and isolation might also affect community composition (beta diversity). Forest management is known to change species assemblages (Aude and Poulsen 2000; Müller et al. 2008; Gossner et al. 2013; Bässler et al. 2014), partly due to altering the habitat availability. Further, different taxonomic groups may not react in the same way, which requires system- and taxon-specific evaluations of the relationship between biodiversity and habitat amount and isolation.

Comparing the responses of multiple taxonomic groups to the same ecological gradient may provide insights on how species groups with different requirements are affected by the amount and spatial

distribution of a given habitat. One may expect taxonomic groups to vary in their response to habitat amount and isolation, for example depending on their dispersal ability, which differs not only between but also within species groups (Komonen and Müller 2018) or even single species (Ronnås et al. 2017). Consequently, selecting the appropriate size of the ‘local landscape’ as mentioned by Fahrig (2013), remains complicated. Only testing responses on one spatial scale might therefore mean that divergent patterns on other scales are overlooked (see Fig. 1). Some previous studies testing the habitat amount hypothesis have considered more than one spatial scale, but the focus has been on the effects of local patch size compared to that of the total habitat amount in the surroundings (Seibold et al. 2017) and fragmentation (Bosco et al. 2019). Habitat isolation, defined as a measure of distance between the sampling site and habitats in the landscape, has not been investigated or, as in a study by Melo et al. (2017), has only been calculated once on a

small scale and not on all scales considered. More studies that include different spatial scales as well as multiple species groups are needed to evaluate the generality of patterns.

In this study, we tested in a forest reserve if habitat amount and/or isolation on different spatial scales (20–200 m radius) are important for biodiversity. In forests, dead wood pieces represent habitat patches with defined borders, scattered in a landscape matrix. We include four species groups, which all depend on dead wood as habitat but have different dispersal strategies and abilities: saproxylic beetles, wood-inhabiting fungi, epixylic bryophytes and epixylic lichens. These species groups make up a considerable part of the total biodiversity in temperate forest systems, are among the groups which show the highest sensitivity to habitat changes caused by forestry (Brunet et al. 2010; Paillet et al. 2010), and are therefore frequently used as indicators for near natural and unmanaged forests (Stokland et al. 2012; Lachat et al. 2012). Intensive management typically reduces the amount and diversity of dead wood, and as a result many species that depend on dead wood are threatened (Martikainen et al. 2000; Grove 2002). Conservation strategies often focus on the amount of dead wood (Jonsson et al. 2005; Müller and Bütler 2010; Halme et al. 2013; Seibold et al. 2015), but some do take the spatial distribution of habitats into account (e.g. Mason and Zapponi 2016). To consider both aspects, we aimed to answer the following questions:

- (1) How is the species richness of saproxylic species associated with dead wood amount and isolation?
- (2) Do the four taxonomic groups show a similar response to dead wood amount and isolation, and are these patterns consistent across different spatial scales?
- (3) Is there a consistent relationship between dead wood amount and isolation and the beta diversity of assemblages across the four investigated taxonomic groups?

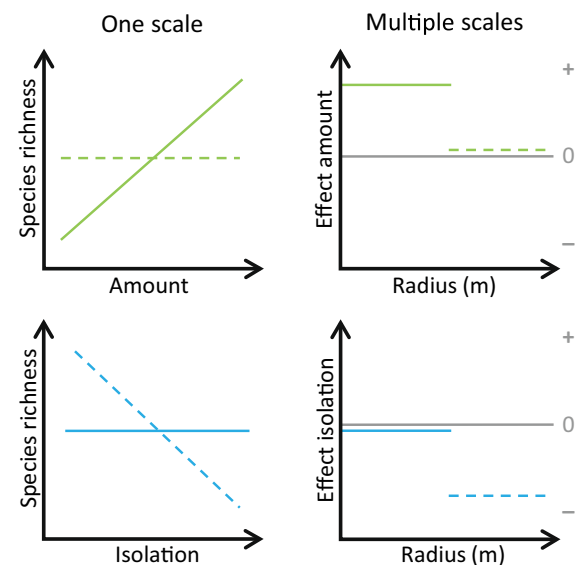


Fig. 1 Possible outcomes showing if the relationship of species richness with dead wood amount (green, top) and isolation (blue, bottom) follow the ‘habitat amount hypothesis’ (HAH). Solid line = consistent with HAH. Dashed line = not consistent with HAH. Left: When considering one scale, a positive effect of amount and no effect of isolation would support the HAH on this scale. Right: The outcome of single scales, i.e. the coefficient estimates of amount and isolation, can be plotted against the tested radii. Here the HAH is supported on smaller scales (positive estimates for amount, no effect of isolation), while it is not supported on larger scales (no effect of habitat amount, negative effect of isolation)

Material and methods

Study area

The study was carried out in the Sihlwald forest reserve (47° 15′ 20″ N, 8° 33′ 00″ E), which is, with

around 1100 ha, the largest continuous unmanaged beech forest in the Swiss lowlands (see Fig. S1 in the Online Resource). The main part of the reserve lies on the northeast-exposed west side of the Sihl river at an elevation of 467–915 m a.s.l. The forest is dominated by European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) (Brang et al. 2011; Brändli et al. 2020). Sihlwald is a young forest reserve (established in 2007) still recovering from over 500 years of intensive management, but there are stands that were left untouched for several decades. Management ceased in 2000, and since 2010 the forest has been protected as a ‘park of national importance’ (MCPFE-category: 1.2).

Plot selection and dead wood map

Our study was based on a subsample of 62 plots selected from 503 permanent forest inventory plots (100 × 200 m raster) established in 1981 and remeasured in 1990, 2003 and 2017. In the latest inventory, all trees with a diameter at breast height (DBH = 130 cm) ≥ 7 cm, tree-related microhabitats (for details see Table S1 in the Online Resource) and dead wood were recorded on circular plots of 300 m² (Brändli et al. 2020). As the natural vegetation of Sihlwald is beech forest and because the focus of our study was dead wood, we only considered plots in mature stands with at least 50% deciduous trees for the selection. This pre-selection was performed using two stand-scale habitat mappings based on aerial imagery [Canton of Zurich (2001) and Wildnispark Zürich (2005)] and resulted in 208 plots.

For the selection of the plots along two orthogonal gradients of dead wood amount and isolation, we created a map of the lying dead wood for the whole perimeter of Sihlwald forest. Following the protocol of Leiterer et al. (2013) a first map was created based on LiDAR data gathered in 2014 (LiDAR laserscanning geodata 1.2.2015, Geographic Information System of the Canton of Zurich). We complemented the LiDAR-based map by digitizing lying dead wood from stereoscopic aerial imagery acquired under leaf-off conditions in 2013 (ADS80 stereo aerial photographs 17.4.2013, swisstopo). We were not able to determine the diameter of the dead wood pieces from the LiDAR data or the stereoscopic aerial images, and we therefore mapped the dead wood as lines.

Based on the dead wood map, dead wood amount and isolation were estimated within a 40 m radius from the center of every plot remaining after the pre-selection (N = 208). This radius was chosen as the ‘local landscape’ because the correlation between dead wood amount and species richness of saproxylic beetles was found to be the strongest in a 40 m radius in a recent study from a temperate European forest (Seibold et al. 2017). We used the summed length of all mapped dead wood pieces within the circle of 40 m radius (Fig. 2) as our estimator of dead wood amount. For dead wood extending beyond the circle, only the part within the circle was considered (see light green lines in Fig. 2). For our estimator of isolation, we calculated the median distance to the plot center of all mapped dead wood pieces within the 40 m radius. We then selected the 62 plots using a stratified random selection along the gradients of dead wood amount and isolation. The minimum distance between two plots was 100 m (Fig. S1).

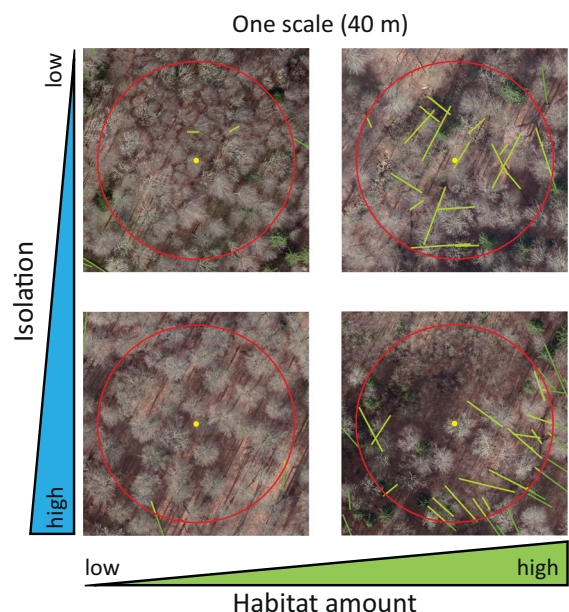


Fig. 2 Four of the 62 selected plots, which differ in dead wood amount (increasing from left to right) and isolation (increasing from top to bottom) on a radius of 40 m around the plot center. Each plot center is indicated by a yellow point. Mapped dead wood pieces are shown as green lines (light and dark green). The circle (solid line) is the 40 m radius used for selection of the plots. Only the parts of dead wood pieces that were within the radius were used to calculate the amount (light green lines). Source: aerial image 17.03.2014, Osterwalder, Lehmann – Ingenieure und Geometer AG

Sampling methods

Beetles were collected from the beginning of May until the middle of August 2017 with two flight interception traps (PolytrapTM) per plot. The traps were emptied every 3rd week. Both traps were situated within a radius of 17.8 m from the plot center and close to a potential habitat, i.e. dead wood (preferably of beech). Species were identified as saproxylic or non-saproxylic based on a list compiled by Müller et al. (2013). Non-saproxylic species were excluded from further analyses. We pooled the species lists of the two traps from each plot for the analyses.

Wood-inhabiting fungi were examined on a 1000 m² circle (17.8 m radius) centered around the plot center. Fungi were recorded based on the occurrence of fruiting bodies: once in autumn (2016), which is the time of year when most fungi have fruiting bodies, and once in June (2017) to detect species with a different phenology. Basidiomycetes and Ascomycetes with fruiting bodies > 0.5 cm in diameter were included.

Bryophytes and lichens were examined on a 314 m² circle (10 m radius) around the plot center from March to June 2017 and from November 2016 to June 2017, respectively. All species were recorded on all substrates, but only epixylic species were included in further analyses. Epixylic bryophytes and lichens were selected on the one hand based on trait information (bryophytes: Landolt et al. 2010; lichens: Stofer et al. 2006; Wirth 2010). On the other hand, species were considered epixylic when they were found on dead wood and had supposedly established on the already dead tissue. These species might not be obligatory epixylic, but they still used the dead wood as habitat. Species that were found on still intact bark of dead wood but that probably established and grew on the tree when it was still alive were considered epiphytic and not epixylic and were therefore excluded from the analyses.

For a detailed examination of fungi, bryophytes and lichens, two dead wood pieces were selected at each plot: the largest log and one randomly selected piece with a diameter between 7 and 12 cm. The two dead wood pieces were located at least partly within the 17.8 m radius around the plot center. For the analyses the species lists of the plot and the dead wood pieces were pooled for each of the three species groups.

Dead wood amount and isolation

The estimators for dead wood amount and isolation for different spatial scales were derived from the dead wood map in the same way as for the 40 m radius used for plot selection. Dead wood amount was calculated as the summed length of all mapped dead wood pieces and isolation was calculated as the median distance from these dead wood pieces to the plot center. For testing the habitat amount hypothesis, Fahrig (2013) proposed using nearest-neighbor distance as the estimator for isolation. As we worked on different spatial scales, we needed a scale-sensitive estimator for isolation which also describes differences in the spatial arrangement of dead wood on larger scales. We therefore used the median distance as a comparable substitute. We calculated the two estimators for each of 19 concentric circles around every plot center ($N = 62$), with the radius of the circles ranging from 20 to 200 m in 10 m steps. With Pearson's r values between -0.3 and 0.01 on the different scales, the two estimators are not correlated (see Fig. S2 in the Online Resource).

Isolation was not included for analyses at a radius of 20 m because the species data were collected in the 1000 m² area (radius = 17.8 m). This radius of 17.8 m included the species inventory on the plot, the two dead wood pieces and the two beetle traps. Calculating isolation as the median distance of all the mapped dead wood pieces to the plot center within the 20 m radius was therefore not reasonable.

Environmental variables

Information about the forest structure on the plot was calculated from the forest inventory (basal area per ha, trees per ha, trees with DBH > 70 cm, maximum DBH, tree species diversity, proportion coniferous trees, tree microhabitats, dead wood diversity) and LiDAR data (tree height, vertical structure). Measurements from the forest inventory, where dead wood was recorded using a transect method (Böhl and Brändli 2007), allowed for the computation of dead wood diversity expressed as the Shannon index for dead wood types based on tree species, diameter class and decay stage. From the transect data the dead wood volume on the plot was estimated following Böhl and Brändli (2007). This volume estimator strongly correlated with the dead wood amount derived from the

dead wood map on small spatial scales (Table S2). We therefore only used the amount derived from the map as our estimator of total dead wood amount for the analyses on all scales, although the volume of coniferous dead wood on the plot was used for the analyses of beta diversity.

Besides forest structure, we measured two abiotic variables. Temperature was measured with one HOBO Pendant® temperature data logger (UA-001-08; Onset Computer Corporation) installed on each plot. Light availability was calculated with the software Hemisfer (Schleppi et al. 2007; Thimonier et al. 2010) from synthetic hemispherical images derived from the LiDAR data (Moeser et al. 2015; Zellweger et al. 2019).

All environmental variables were independent of scale, while the values for dead wood amount and median distance changed with spatial scale. Details on all variables are provided in the Online Resource (Table S1).

Species richness

To assess the response of species richness to dead wood amount and isolation across spatial scales, we first specified a full model for every radius (20–200 m, 10 m steps) for each taxonomic group. Species richness was the response variable in the models. Dead wood amount (20–200 m radius) and isolation (30–200 m radius) from the respective radius and—to ‘filter out’ their potential effects—the scale-independent environmental variables were used as explanatory variables (Table S1). All explanatory variables were centered at 0 and scaled to SD = 1. All statistical analyses were performed using R Version 3.5.2 (R Core Team 2018).

We used generalized linear models (GLMs) with a negative binomial distribution (function *glm.nb*, package ‘MASS’; Ripley et al. 2018), as initial analysis with poisson models showed overdispersion. We then performed model selection based on the corrected Akaike information criterion (AICc) to identify the best model containing both focal variables (dead wood amount and isolation) on each scale using the function *dredge* (package ‘MuMIn’; Barton 2018). The best model for different scales could—besides dead wood amount and isolation—include different variables. We aimed at assessing the relative importance of dead wood amount and isolation across spatial scales and

did not assess effect size. For every species group and every radius, we report coefficient estimates, standard errors, z-values and p-values of the best model in the Online Resource (Tables S3–S6). Additionally, we present the R^2 values (likelihood-ratio based) in Table S7.

Beta diversity

We calculated the Sørensen index (total beta diversity) to determine the dissimilarities between communities on the plot. For each of the species groups, we calculated the multi-site dissimilarities (beta.SOR, beta.SIM, beta.SNE) with the function *beta.multi* and averaged the pairwise dissimilarities (beta.sor, beta.-sim, beta.sne), calculated with the function *beta.pair* (R package ‘betapart’; Baselga et al. 2017).

We performed generalized dissimilarity modeling (GDM) to analyze which factors explain changes in community composition, represented by the Sørensen index (beta.sor) (*gdm* function, package ‘gdm’; Manion et al. 2018). We used the same explanatory variables as for the analyses of species richness (Table S1), but we added one variable describing the volume of coniferous dead wood on the plot (derived from the inventory data) because communities of saproxylic species are known to differ between deciduous and coniferous dead wood. Further, the geographic distance between plots was included as a variable in the models.

The GDMs were performed on every scale between 20 and 200 m radius (10 m steps), keeping the environmental variables unchanged while using the values for dead wood amount and isolation for the respective radius. Using the full models including all predictor variables, we calculated the importance of each variable in 50 permutations (*gdm.varImp* function, package ‘gdm’; Manion et al. 2018). Based on these results, we only included variables explaining more than 1% of deviance on at least one scale to obtain less complex models for each species group. The environmental variables included in the small models were therefore the same for all the scales within each species group. Dead wood amount (20–200 m radius) and isolation (30–200 m radius) were always included, regardless of their importance. We then estimated overall deviance explained, variable importance and p-values once more for the small

models on all scales with the *gdm.varImp* function (see Online Resource, Tables S9–S12).

Results

In total, we found 327 beetle, 387 fungal, 74 bryophyte and 35 lichen species associated with dead wood on the 62 plots (Table 1). The proportion of species that were only found on one plot ranged from 21% (beetles) to 46% (lichens).

Species richness

For each species group, we found significant positive relationships between dead wood amount and species richness, but the species groups differed in the spatial scales at which this effect manifested (Fig. 3, Tables S3–S6). For fungi, bryophytes and lichens, significant positive effects of dead wood amount occurred at smaller radii (up to 60 m for fungi, 40 m for bryophytes, 80 m for lichens) but not at larger radii (Fig. 3b–d). The strongest effects were found at 30 m for fungi, 40 m for bryophytes and 50 m for lichens. In contrast, species richness of beetles increased with increasing dead wood amount on all spatial scales. Further, the magnitude of this effect was constant across scales (Fig. 3a) and the effect was significant at all radii.

The responses to isolation showed different patterns for fungi, bryophytes and lichens compared with that for the beetles (Fig. 3). We found fewer species of fungi, bryophytes and lichens with increasing isolation on larger scales. The negative relationship started

being significant on scales between 60 and 100 m and despite not being significant on all larger scales, the pattern remained consistent for fungi, bryophytes and lichens. In contrast, for beetles there was no consistent relationship between species richness and isolation on any scale.

The proportion of variance explained by the best model on each scale, ranged from 30.3% (50 m) to 34.9% (140 m) for beetles, from 31.4% (70 m) to 41% (40 m) for fungi, from 36.7% (150 m) to 45.3% (30 m) for bryophytes and from 20.1% (180 m) to 40.5% (130 m) for lichens (values for all scales are reported in Table S7).

Beta diversity

Species assemblages of all taxonomic groups showed a similar and high multi-site community dissimilarity (around 95%), and most of the dissimilarity (over 90%) was due to species turnover and not nestedness (Tables 2 and S8). When looking at the averaged pairwise dissimilarity, the groups showed larger differences. While the average dissimilarity between two plots was lowest for beetles (44%), it was highest for fungi (82.4%).

The generalized dissimilarity models (GDMs) explained up to 13.5% of the difference in community composition for lichens and up to 16.2% for beetles. For fungi (max. 6.2%) and bryophytes (max. 3.3%) this fraction was much lower (Table 2, values for all scales see Table S9).

The effect of dead wood amount on community composition was only significant for fungi on larger spatial scales (130 m, 170 m and 200 m) (Fig. 4b,

Table 1 Species richness of the four species groups on the 62 plots

	Saproxyllic beetles	Wood-inhabiting fungi	Epixylic bryophytes	Epixylic lichens
Total				
Number of species	327	387	74	35
Singletons (percent)	67 (20.5%)	166 (42.9%)	18 (24.7%)	16 (45.7%)
Per plot				
Min.	41	7	4	0
Mean \pm SD	79.6 \pm 15.8	29.1 \pm 10.5	15.6 \pm 5.8	2.3 \pm 1.9
Max.	116	55	31	8

Species identified only to the genus level were excluded. Singletons were defined as species found on only a single plot, independent of their abundance on that plot

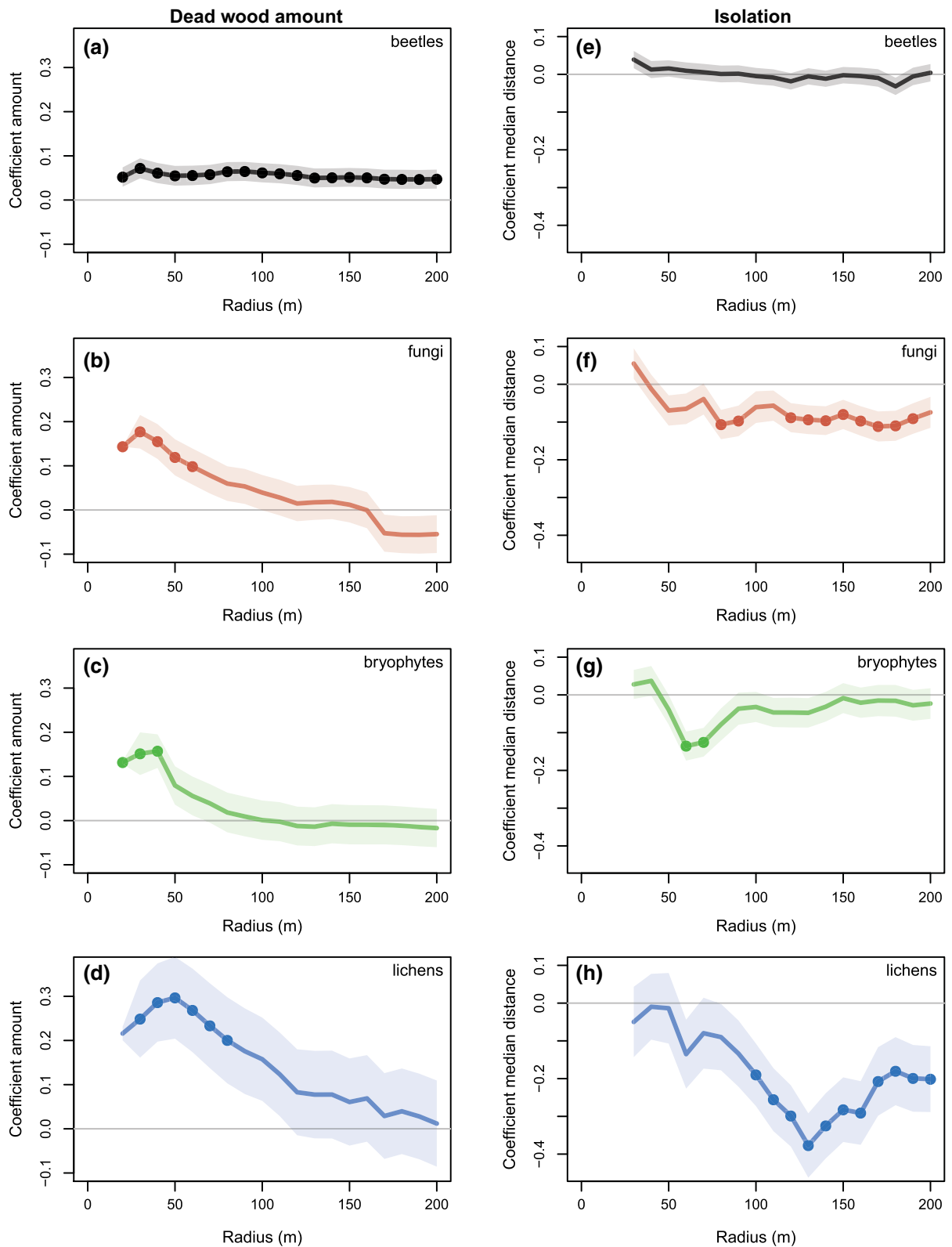


Fig. 3 Coefficient estimates of dead wood amount (summed length of dead wood pieces; left) and isolation (median distance of dead wood pieces to the plot center; right) derived for beetles (a, e), fungi (b, f), bryophytes (c, g) and lichens (d, h) from the best model of the respective scale. line = coefficient estimate, dot = $p < 0.05$, band = standard error

Table S11). The species assemblage changed with an increasing amount of dead wood but reached a plateau soon thereafter: a larger amount after this point did not lead to a different community composition. The effect of isolation on community composition was only significant for the two species groups with the highest explained variance in the GDM: once for lichens (50 m) and twice for beetles (170 m and 180 m) (Fig. 4, Tables S10 and S13).

Discussion

The diversity of the four studied species groups (saproxylic beetles, wood-inhabiting fungi, and epixylic bryophytes and lichens) was associated with dead wood amount and isolation on different scales. Even though the species groups differed in total species numbers, with high numbers for beetles (327) and fungi (387) and much lower numbers for bryophytes (74) and lichens (35), we found similarities in their responses to amount and isolation. Contrasting patterns became apparent on different spatial scales for the four taxonomic groups, highlighting the importance of multi-scale testing and a multi-species

approach. In particular, we found that the amount of dead wood was important in explaining the diversity on a small spatial scale, while isolation became more important on larger spatial scales.

Species richness increased with dead wood amount across a range of spatial scales. On small scales (radius < 60 m), our results were similar for the taxonomic groups and all four groups showed a positive relationship. Dead wood amount was always more important than isolation, which is consistent with the habitat amount hypothesis (Fahrig 2013). A positive relationship at the 20 m radius might be partly explained by the larger amount of local dead wood that was actually examined for fungi, bryophytes and lichens (species–area relationship). However, the coefficients of dead wood amount did not peak at 20 m for any of the groups, showing that this should not interfere with our results. Our results are further consistent with previous studies on saproxylic species showing a positive effect of dead wood in the immediate surroundings on species richness (e.g. Lassauce et al. 2011; Boch et al. 2013; Müller et al. 2015; Seibold et al. 2017). This suggests that the studied taxonomic groups are not dispersal limited on smaller spatial scales.

Different responses of the species groups to dead wood amount and isolation were only evident on larger scales. As especially the difference of beetles compared with fungi, bryophytes and lichens became apparent (Fig. 3), the responses might be explained by different dispersal abilities and strategies.

For beetles the habitat amount was always more important than its spatial distribution. The coefficient

Table 2 Dissimilarities of community composition of the four species groups

	Saproxylic beetles	Wood-inhabiting fungi	Epixylic bryophytes	Epixylic lichens
Multi-site dissimilarity β_{SOR}	93.5%	96.9%	94.3%	96%
Pairwise dissimilarity β_{SOR}	44 ± 5.4%	82.4 ± 8.9%	50.1 ± 12.2%	73.4 ± 27.4%
Explained variance (GDM) ^a				
Min	13.5% (120 m)	3.6% (40 m)	2.1% (150 m)	10.9% (90 m)
Max	16.2% (170 m)	6.2% (180 m)	3.3% (60 m)	13.5% (60 m)

Multi-site dissimilarity (rounded): overall dissimilarity (Sørensen index). Pairwise dissimilarity (rounded): mean of total dissimilarities between two plots ± standard deviation (SD). Explained variance (rounded): proportion of the variance in community composition that could be explained by the generalized dissimilarity models (small models). Shown are the radii (m in brackets) with the lowest and the highest proportion of explained variance

^aValues from 20 m radius were excluded, as the models include one variable less (isolation); for fungi (3.6%), bryophytes (2.1%) and lichens (10.7%) explained variance was the lowest on 20 m radius

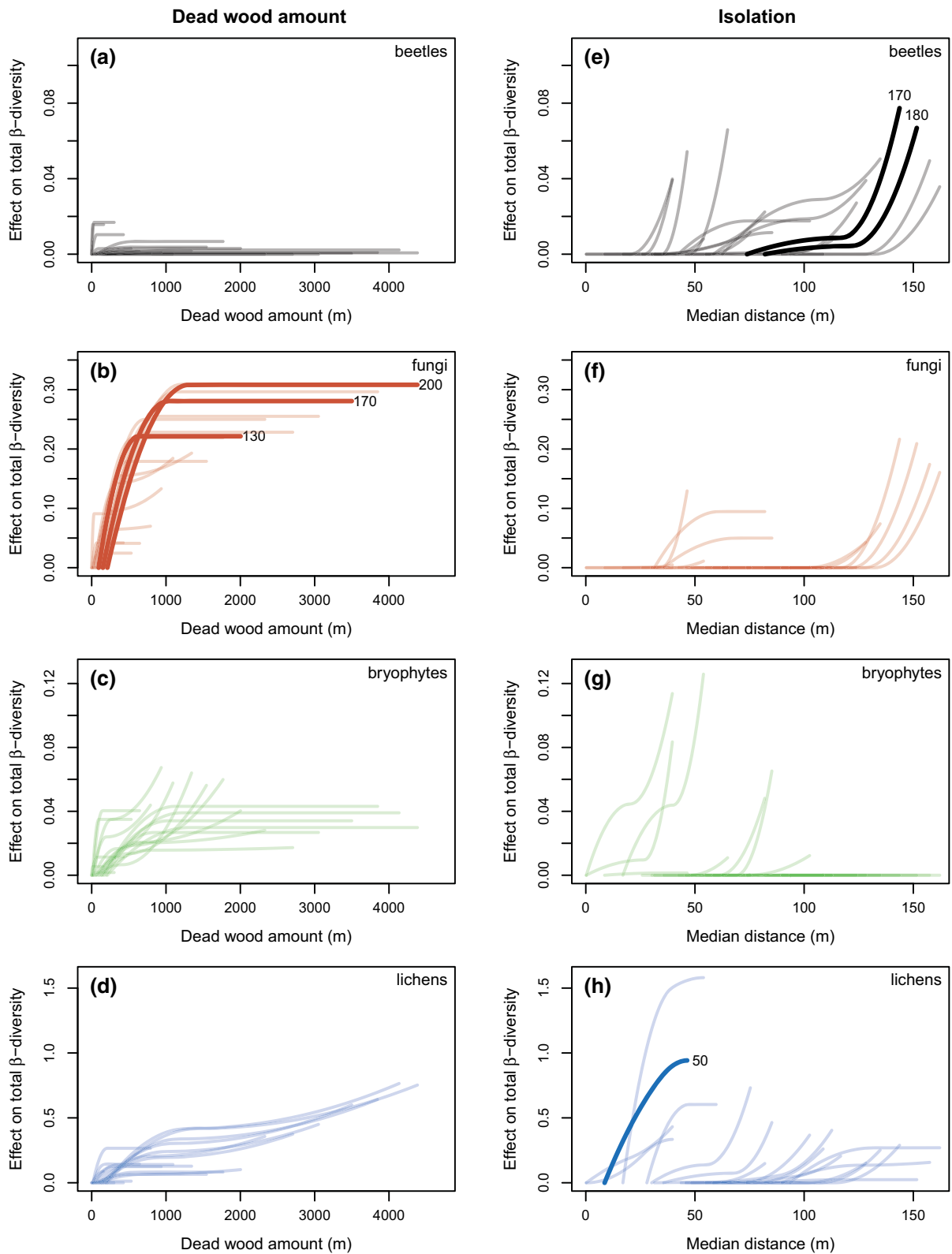


Fig. 4 Results of generalized dissimilarity modeling from the small models for the four species groups: beetles (**a, e**), fungi (**b, f**), bryophytes (**c, g**) and lichens (**d, h**). The shape of the curves (I-splines) indicates the effect of dead wood amount (summed length of dead wood pieces; left) and isolation (median distance of dead wood pieces to the plot center; right) along their gradients on changes in community composition (beta diversity). The strength of the effect is indicated by total curve height (for absolute values see Tables S10–S13). One line represents one spatial scale. Lines for each scale differ in their start/end and length on the x-axis because the gradient of the variable depends on the scale (e.g. dead wood amount 50 m radius: 12.5–531.4 m, 100 m radius: 54.3–1344.0 m). Bold lines are I-splines of amount or isolation when the variable was significant ($p < 0.05$) on the respective scale (radius indicated next to the line). Note that the y-axis scale differs among species groups

of dead wood amount remained constant and positive from 20 to 200 m radius, while isolation showed no relationship with species richness on any scale. Many saproxylic beetle species are considered highly mobile, capable of flying longer distances to colonize new habitats, and are therefore considered unimpaired by dispersal limitations (Ranius 2006; Janssen et al. 2016; Komonen and Müller 2018). Besides having a scattered distribution, dead wood is an ephemeral and dynamic habitat (Saint-Germain et al. 2007; Jönsson et al. 2008; Caruso et al. 2010). Consequently, not every dead wood piece meets the ecological requirements of every species (e.g. tree species, dimension or decay stage) at all times (Grove 2002; Stokland et al. 2012). Beetles can actively direct their movements to detect suitable habitat, allowing for easier colonization of dead wood within their movement range and beyond their immediate surroundings (Jonsson and Nordlander 2006; Vandekerkhove et al. 2011). Yet, depending on the stability of the respective suitable habitats (from stable cavities to more ephemeral fresh dead wood) different saproxylic beetle guilds were shown to be affected by landscape structure on different scales (Percel et al. 2019). Our results should therefore not lead to the conclusion that the spatial distribution of dead wood in the landscape is never important for saproxylic beetles. Negative effects may occur on larger spatial scales than those included in this study (Sverdrup-Thygeson et al. 2014) and/or for species with lower dispersal abilities (e.g. some red listed species: Brunet and Isacsson 2009; Rossi de Gasperis et al. 2016).

In contrast to the patterns observed for beetles, the significant relationship between dead wood amount and species richness of fungi, bryophytes and lichens disappeared on larger spatial scales in our study (radius > 60 m). Instead, isolation showed a negative correlation with the species richness of these three species groups. This result contradicts the habitat amount hypothesis and suggests that the importance of habitat amount is scale dependent and that isolation is more important on larger scales. These species groups are considered sessile but disperse passively through propagules (lichens and bryophytes) or spores (fungi, bryophytes and lichens), which in principle enables airborne long-distance dispersal (Kallio 1970; Frahm 2007; Lönnell et al. 2014; Gjerde et al. 2015; Ronnås et al. 2017; Abrego et al. 2018; Komonen and Müller 2018). One could therefore expect that these species groups are not dispersal limited. However, it has been shown for fungi that spores principally disperse in the vicinity of sporulating fruiting bodies, because spore density rapidly decreases with increasing distance (Gregory 1945; Nordén and Larsson 2000; Edman et al. 2004; Norros et al. 2012). High spore densities up to around 100 m (Nordén and Larsson 2000; Norros et al. 2012) increase the chances that spores land on a suitable dead wood resource, if one is present. Similarly, dispersal limitations on the local scale have been found for various bryophyte and lichen species, probably because the vegetative propagules are often dispersal limited and settle mostly close to the source (Löbel et al. 2006; Werth et al. 2006; Scheidegger and Werth 2009; Lönnell et al. 2014). This could explain the negative relationship between species richness and isolation on the larger scales of this study. Still, species richness of bryophytes has been found to have a stronger response to habitat/source amount in the landscape than to the distance to the next source, probably due to a higher spore background level (Hylander 2009; Sundberg 2013). Conservation measures for promoting species richness of multiple taxonomic groups with different dispersal strategies and abilities should thus consider the amount of dead wood, as well as its spatial distribution in the landscape.

The response of community composition to dead wood amount and isolation was less clear. Even though it is known that forest variables influence community composition of the four species groups studied here (Löbel et al. 2006; Tinya et al. 2009;

Raabe et al. 2010; Gossner et al. 2013; Vodka and Cizek 2013; Heilmann-Clausen et al. 2014), we could not explain most of the variance in the compositional dissimilarity (Tables 2, S9). Overall, we could not confirm our assumption that an increasing amount of dead wood would lead to different species assemblages. Such a pattern was only seen for fungi on three spatial scales (Fig. 4b) and the total deviance explained by the GDMs stayed low also on these scales (max. 6%). Wood-inhabiting fungi often show over-dispersed community assemblages (Bässler et al. 2014) and therefore more dissimilarities between communities compared with other species groups, e.g. bryophytes (Heilmann-Clausen et al. 2005). This might be explained by strong competition between fungi in single dead wood pieces, with the consequence that only a few species build fruiting bodies (Heilmann-Clausen and Christensen 2004; Fukami et al. 2010; Roth et al. 2019). Probably due to these processes, other studies on wood-inhabiting fungi likewise did not show a relationship between local dead wood amount and community composition (Krah et al. 2018) or changes in composition 10 years after dead wood enrichment (Roth et al. 2019). In contrast, Raabe et al. (2010) found an effect of local dead wood amount on the community composition of epixylic bryophytes, and the models they used managed to explain 21% of the variance, a value our models did not reach. Besides dead wood amount, also isolation could not be identified as having a strong influence on community composition, being only significant on a few scales and lacking consistent patterns. For saproxylic beetles the findings of a previous study in Sihlwald forest, where community composition changed with connectivity (nearest-neighbor distance) but not with total dead wood volume (Schiegg 2000), were partly supported by our results. The effect of isolation was indeed greater than that of dead wood amount on most scales. Nevertheless, this finding should not be overrated, as the effect was only significant on two scales and not consistent. The absence of strong effects explaining community composition in this study might be a consequence of the spatial scales we studied (20–200 m radius). On larger scales it has previously been shown that, for example, the community composition of saproxylic beetles differed along a gradient of the proportion of old forest within 1, 2 and 3 km (Olsson et al. 2012).

Further, Sihlwald forest is still very homogeneous, as it is a young forest reserve in the optimum stage of forest succession. Diversity of dead wood (e.g. different decay stages), which is important for the community composition of saproxylic species, might thus still be low. On the stand scale, differences in species assemblages caused by larger dead wood amounts might therefore only be found during a short time period after fresh dead wood is created, when early colonizers appear (Komonen et al. 2014). Hilmers et al. (2018) showed that assemblages of many species groups (including beetles, fungi, bryophytes and lichens) change along a forest succession gradient, with the most unique species appearing during early and/or late successional forest stages. Changes in community composition therefore might have a stronger relationship with forest variables and dead wood when the forest becomes more heterogeneous and gradients more pronounced.

Conclusions

Regarding the habitat amount hypothesis, selection of the ‘appropriate’ scale still remains one of the largest challenges (Fahrig 2013). While habitat amount, but not isolation, was important for all of the four investigated species groups (saproxylic beetles, wood-inhabiting fungi, and epixylic bryophytes and lichens) on small scales, the inverse pattern occurred on larger spatial scales for three of the species groups (fungi, bryophytes and lichens). Although previous studies have suggested that the spatial scales at which habitat amount and isolation affect species richness may differ, we present evidence that such patterns may be a widespread phenomenon. Importantly, if we had strictly followed the recommendations of Fahrig (2013) by choosing the radius with the strongest relationship between species richness and habitat amount as the ‘local landscape’, we would have incorrectly inferred the complete absence of isolation effects. Further, our findings demonstrate that patterns valid for one species group cannot automatically be projected onto other species groups, even though they use the same habitat.

Our results on the effects of dead wood amount and its spatial distribution can be of help for the conservation of saproxylic species in forest ecosystems. Based on our findings, the priority should be given to

increasing the quantity of dead wood. In managed forests, one way this can be achieved is through retaining tree crowns after logging. When establishing new protected areas like forest reserves in formerly managed forests, targeted measures enhancing dead wood quantities can speed up the restoration process. Acknowledging that the spatial arrangement of dead wood already affects species richness within a forest reserve like the Sihlwald, it should be considered where applicable. A broad application of such measures will lead to the enhancement and even distribution of dead wood on both the forest and the landscape scale, increasing the availability of this important habitat for forest biodiversity.

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